THE THEORY OF INSULAR BIOGEOGRAPHY AND
THE DISTRIBUTION OF BOREAL BIRDS AND MAMMALS

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Abstract.—The present paper compares the distribution of boreal birds and mammals among the isolated mountain ranges of the Great Basin and relates those patterns to the developing theory of insular biogeography. The results indicate that the distribution of permanent resident bird species represents an approximate equilibrium between contemporary rates of colonization and extinction. A shallow slope of the species-area curve ($Z = 0.165$), no significant reduction in numbers of species as a function of insular isolation (distance to nearest continent), and a strong dependence of species diversity on habitat diversity all suggest that immigration rates of boreal birds are sufficiently high to maintain populations on almost all islands where there are appropriate habitats. In contrast, the insular faunas of boreal mammals represent relictual populations that receive no significant contemporary immigration. The insular mammal faunas have been derived by extinction from a set of species that colonized the islands when habitat bridges connected them to the continents in the late Pleistocene. A relatively steep species-area curve ($Z = 0.326$), no effect of isolation on species diversity, and the absence of appropriate species from large areas of apparently suitable habitat all support this conclusion. Measures of habitat diversity that are closely correlated with bird species diversity do not account for much of the variation in number of mammal species among islands. Insular area is the single variable that accounts for most of the variability in both bird and mammal species diversity; this supports the approach of using standard parameters such as area in comparative empirical analyses and general biogeographic theory. The results of this study suggest that extremes of vagility among taxa and a recent history of paleoclimatic and geological changes make it unlikely that equilibrial distributions, of the sort MacArthur and Wilson (1967) propose for the biotas of oceanic islands, are characteristic of the insular distributions of terrestial and freshwater vertebrates of western North America.

Biogeography is an old science that has made recent advances by assimilating new concepts and data. Within the last two decades information on continental drift, paleoclimatology, and ancient sea levels has revolutionized our understanding of historical events and their effects on plant and animal distribution. During the same period, ecologists and evolutionary biologists have learned much about the processes of population growth, dispursal, extincton, speciation, and interspecific interactions which are the mechanisms that determine distribution. Biogeography appears to be entering an exciting new period in which the voluminous data acquired by systematists and descriptive biogeographers can be interpreted in terms of recently understood historical events and ecological processes to draw quantitative relationships and derive general principles.

With the publication of their equilibrium model of insular distribution, MacArthur and Wilson (1963, 1967) contributed not only a new theory but also a new approach to biogeography. Prior to their work, most biogeographic research had consisted of describing the distributions of particular taxa and producing ad hoc, historical explanations. MacArthur and Wilson advocated a quantitative approach designed to build and test general models based on ecological processes. The specific model that they proposed suggests that the number of species inhabiting an island represents an equilibrium between opposing rates of extinction and colonization, and that these processes are functions of the size of an island and its

distance from a source of colonists, respec- tively.

MacArthur and Wilsons's choice of is lands for their revolutionary approach to biogeography was not a fortuitous one. Ever since the pioneering work of Darwin and Wallace, islands have played a preeminent role in the development of the science. It is difficult to do experiments in biogeography, but islands and insular habitats represent natural experiments; they are small, replica ted systems among which species and envi ronmental parameters are distributed in dif ferent combinations. Often particular taxa are distributed among insular habitats in patterns that imply the operation of general mechanisms of dispersal, extinction, and in terspecific interaction. The last decade has seen several attempts to test the model of MacArthur and Wilson, using a variety of organisms that inhabit both true islands and analogous isolated habitats (e.g., Barbour and Brown 1974, Brown 1971, Brown and Kodric-Brown in review, Culver 1970, Cul ver et al. 1973, Diamond 1969, 1970a, 1971, Johnson 1975, Harper et al. this sym posium, Schoener 1974, Seifert 1975, Sim berloff 1974, Simberloff and Wilson 1970, Simpson 1974, Terborgh 1973, Vuilleumier 1970, 1973). Not all of these studies have supported the model, but the exceptions have contributed importantly to our under standing of the patterns of insular distribu tion and the historical events and ecological processes that produce them.

Analysis of the distribution of vertebrates among isolated habitats in the Inter mountain Region of western North America has contributed significantly to the devel opment and testing of biogeographic theory. The dedicated field work of several gener ations of systematists has documented in de tail the species distributions of most verte brate groups (e.g., for fishes Miller 1948, Hubbs and Miller 1948, Hubbs et al. 1974, Smith, this symposium; for birds Behle 1943, 1955, 1958, this symposium, Grinnell and Miller 1944, Johnson 1965, 1970, 1973, 1974, 1975, Linsdale 1936, Miller 1935,

1946, Miller and Russell 1956, Van Ros sem 1936; for mammals Durrant 1952, Dur rant et al. 1955, Grinnell 1933, Hall 1946). The paleoclimatic history of the region also is becoming increasingly well understood (e.g., Hubbs and Miller 1948, Martin and Mehringer 1965, Smith this symposium, Wells and Berger 1967, Wells and Jorgen sen 1964). This excellent data base has been used in quantitative analyses of the insular distributions of lacustrine fishes (Barbour and Brown 1974) and montane birds (John son 1975) and mammals (Brown 1971). Much more work remains to be done. Some of the most interesting contributions can be expected when additional kinds of organ isms and insular habitats are studied, so that it is possible to make comparisons among taxa which differ in ecological requirements and dispersal abilities, and among habitats that differ in environmental parameters and history of isolation.

The present paper discusses the distribu tion of boreal birds and mammals among isolated mountain ranges in the Great Basin in relation to the theory of insular bio geography. It attempts to relate distribu tional patterns to mechanisms of dispersal and extinction and to differentiate relictual patterns that are the legacy of historical events from equilibrial ones that can be at tributed to contemporary ecological pro cesses. The paper tries to develop a general conceptual basis for analyzing and predict ing insular distributions. It first discusses the current state of insular biogeographic theo ry and then utilizes empirical data on the distribution of boreal birds and mammals to test the theory and search for general mech anisms.

THE THEORY OF INSULAR BIOGEOGRAPHY

Colonization, extinction, and speciation are the primary processes that determine the composition of insular biotas. An island can be defined as a patch of suitable habitat surrounded by unfavorable environment that limits the dispersal of individuals. New spe-

cies colonize an island either by dispersing across the habitat barriers or by immigrating sometime when the barriers were temporarily absent. Speciation entirely within an island potentially is another source of new species, but there is no evidence that this process has contributed significantly to the diversity of boreal birds and mammals in the Great Basin region. Extinction, which may be caused by a variety of factors that reduce population size, eliminates species and reduces insular diversity. The composition of an insular biota is determined by the interaction of these origination and extinction processes.

MacArthur and Wilson (1963, 1967) developed a simple, general model of insular biogeography that represents the number of species inhabiting an island as an equilibrium between contemporary rates of colonization and extinction (Fig. 1). Their model makes the colonization rate a decreasing function of distance to a source of dispersing species (usually the nearest continent) and extinction rate a decreasing function of island size. The model predicts: first, that relatively constant insular species diversity is maintained by the continual turnover (extinction and colonization) of individual species; second, that the equilibrium number of species is positively correlated with island size and negatively correlated with distance to the source of potential colonists; and third, that the equilibrium turnover rate is inversely related to both island size and distance to a source of species. Although the MacArthur-Wilson model was designed specifically to account for the diversity of organisms on oceanic islands, it has proven a useful heuristic device for analyzing many kinds of insular distributions because it deals with general processes and makes robust, testable predictions.

As the MacArthur-Wilson model has been tested using a variety of taxa distributed among both oceanic islands and several kinds of insular habitats (see references cited above), it has become increasingly clear that in its present form it is inadequate to account for many empirical ex-
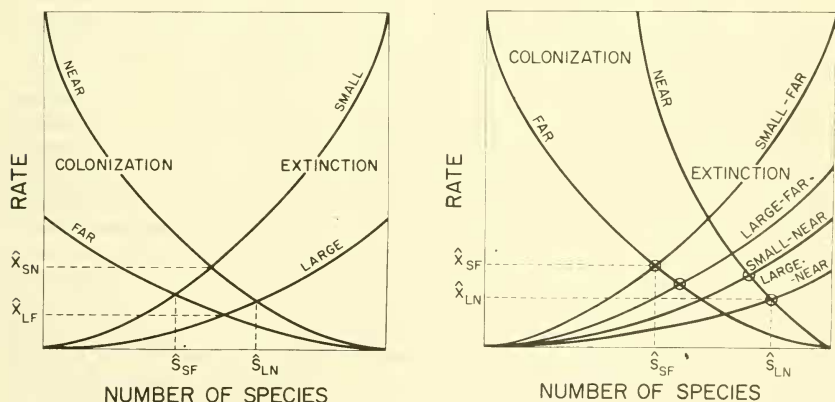

Fig. 1. Two models of equilibrium insular biogeography. Left, the MacArthur-Wilson model, which portrays extinction and colonization rates as functions of island size and isolation respectively. Right, a modification of the MacArthur-Wilson model by Brown and Kodric-Brown (1977), which incorporates the effect of insular isolation on extinction rate. In both models intersections of the curves can be extrapolated to the abscissa and ordinate to give equilibrial numbers of species ($\hat{S}$) and turnover rates ($\hat{X}$), respectively. Note that the two models predict the same relative order of numbers of species but different orders of turnover rates with respect to island size and isolation.

amples. Two major problems have arisen in attempts to use the model to account for empirical patterns of animal and plant distribution. First, in some insular habitats, historical episodes of immigration, speciation, and extinction have produced numbers of species that are significantly greater or less than the equilibrial number expected on the basis of contemporary rates of colonization and extinction (Barbour and Brown 1974, Brown 1971, Culver et al. 1973, Diamond 1970). Such historically determined distributions should be particularly common in organisms that are poor dispersers (such as the small, nonflying vertebrates) and in geographic areas (such as western North America) where paleoclimatic and geological changes have drastically altered the barriers that currently isolate insular habitats. Second, it has proven difficult to test the Mac-Arthur-Wilson model's critical predictions about insular turnover. Although it is relatively easy to census accurately the biota of an island, it is much more difficult to assess the natural turnover rate. As a result, most of the purported measures of insular turnovers have been criticized (see Diamond 1969, 1971, Terborgh 1973, Lynch and Johnson 1974, Simberloff 1974), and the critical predictions of how turnover rate varies with island size and isolation remain untested. Recently, Brown and Kodric-Brown (1977) obtained empirical evidence that insular extinction rates may be strongly dependent on the distance of an island from a source of colonists, rather than on island size alone as MacArthur and Wilson suggest. Areas that are sources of colonizing species often also may be sources of immigrant individuals of species already present on the island; the arrival of these immigrants may refuce the probability that insular populationd go extinct. We predicted that, for many islands, species turnover rates are lower for islands near sources of dispersing species than for more isolated ones. Although this is the opposite of the pattern predicted by the MacArthur-Wilson model, the model can easily be modified to in-

corporate this influence of immigration on extinction rate (Fig. 1).

Neither of these problems detracts from the utility of MacArthur and Wilson's model as a heuristic device or the value of their approach. Their work did much to stimulate biogeographers to develop precise hypotheses and test them with appropriately analyzed quantitative data. Gradually a conceptual understanding of insular biogeography is emerging that may not be as simple and elegant as the MacArthur-Wilson model, but it is hoped it will be more realistic. In the following sections, I hope to use the distribution of boreal birds and mammals among isolated mountain ranges in the Great Basin to illustrate this theoretical approach and some of the resulting concepts.

MONTANE ISLANDS

The mountain ranges of the Great Basin are islands of coniferous forest and associated mesic habitats in a sea of desert. The Great Basin is a vast interior drainage that lies between two montane continents, the central mountains of Utah (a part of the Rocky Mountains) on the east and the Sierra Nevada on the west (Fig. 2). Most of this area consists of broad arid valleys, which lie at an elevation of approximately 5000 feet and are sparsely covered with a vegetation dominated by low woody shrubs of the genera *Artemisia*, *Chrysothamnus*, and *Atriplex*. Between the valleys are a series of mountain ranges oriented in a north-south direction. Many of these rise to over 10,000 feet; on their lower slopes they are covered with juniper-pinyon woodland and at higher elevations there are forests of mixed conifers, stands of aspens, and sometimes wet meadows and permanent streams.

The present analysis is based on 19 islands for which the boreal mammal fauna is adequately known; lists of boreal bird species are available for 13 of these. Islands were defined by operational criteria applied to topographic maps (U.S. Geological Sur-

vey maps of the states: scale 1:500,000). A montane island was considered to be a mountain range that contains at least one peak higher than 9800 feet and is separated from other highland areas by a valley at least 5 miles across below an elevation of 7500 feet. This altitude represents the approximate lower boundary of juniper-pinyon woodland. For each island, area above 7500 feet elevation, distance to nearest continent (Sierra Nevada or central mountains of Utah), and elevation of highest peak were determined from topographic maps (Table 1). For 13 islands ornithologists (Johnson 1975, Behle, this symposium) have quantified the diversity of habitats available to boreal birds. This habitat diversity score incorporates the number of coniferous tree species and the presence of riparian woodland, wet meadow, and aquatic habitats (see Johnson 1975 for details). Since West (this symposium) has shown that juniper-pinyon woodland is absent or poorly developed in the northern Great Basin, the islands selected for this analysis lie south of the Humboldt River and Great Salt Lake to insure that they have somewhat comparable habitats.

BOREAL BIRDS AND MAMMALS

For the bird and mammal species that are restricted to juniper-pinyon woodland and more mesic habitats of higher elevations, the mountains of the Great Basin are truly islands. Their boreal avian and mam-

TABLE 1. Data for the boreal habitats used in the present analysis.

Great Basin Montane "Islands"	Area above 7,500 feet (sq. miles)	Highest peak (feet)	Nearest continent (miles)	Habitat diversity score[1]	Permanent resident bird species[2]	Small Boreal mammal species[3]
1. White-Inyo	738	14,242	10	11	8	11
2. Panamint	47	11,045	52	3	5	3
3. Desatoya	83	9,814	83	2	4	7
4. Toiyabe-Shoshone	684	11,788	110	7	6	13
5. Toquima-Monitor	1,178	11,949	114	—	—	10
6. Roberts Creek	52	10,133	216	—	—	4
7. Diamond	159	10,614	190	—	—	4
8. Ruby	364	11,387	173	9	6	12
9. Spring	125	11,918	125	7	6	6
10. Sheep	54	9,912	86	5	5	3
11. Grant-Quinn Canyon	150	11,298	138	9	5	5
12. White Pine	262	11,188	150	—	—	7
13. Schell Creek-Egan	1,020	11,883	114	—	—	8
14. Spruce-South Pequop	49	10,262	156	4	4	4
15. Snake	417	13,063	89	14	9	10
16. Deep Creek	223	12,101	104	11	7	8
17. Pilot	12	10,704	114	—	—	3
18. Stansbury	56	11,031	39	8	6	6
19. Oquirrh	82	10,626	19	9	6	6
Sierra Nevada Mainland						
20. Carson	284	10,788	0	17	13	22
21. Yosemite	828	13,090	0	18	15	23
Rocky Mountain Mainland						
22. Paunsaugunt-Aquarius	1,008	11,124	0	14	13	16
23. Uinta	1,536	13,498	0	15	14	21

[1] From Johnson (1975) and Behle (this symposium).
[2] See Appendix 1 for documentation.
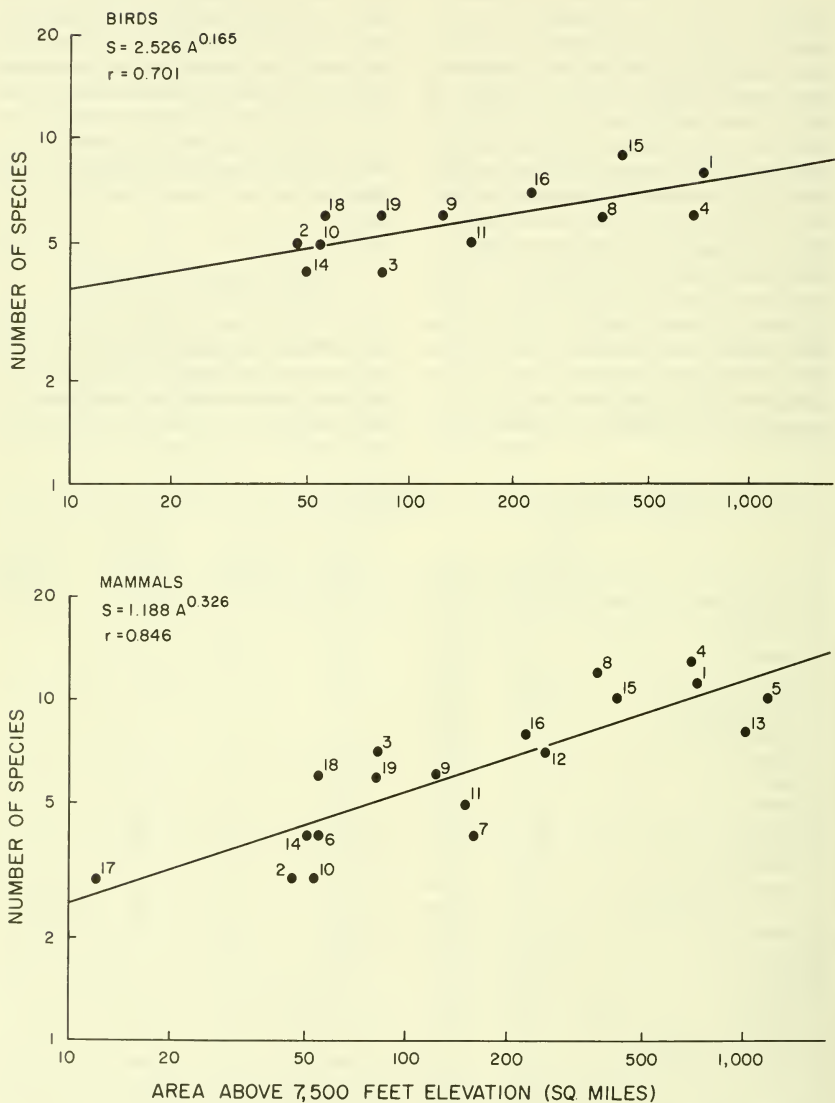[3] See Appendix 2 for documentation.

Fig. 2. Map of the Great Basin region of western North America showing the location of the isolated mountain ranges used in the present analysis. Numbers refer to individual montane islands and continental sample areas listed in Table 1. Note that islands of varying size and isolation lie in the "sea" of desert habitat between the central mountains of Utah on the east and the Sierra Nevada of California on the west.

malian faunas are depauperate subsamples of the Sierra Nevada and Rocky Mountain faunas. All of the bird and mammal species that inhabit the isolated peaks are broadly distributed on one or (more frequently) both of the continental ranges to the east and west (see appendix and references cited there), but a significant proportion of the continental species are not present on any particular island and some are absent from all islands. The continental mountain ranges clearly are the source of the insular boreal faunas, and the distribution of species on the islands is the result of their abilities to colonize and avoid subsequent extinction.

The definition of boreal bird and mammal species is somewhat arbitrary, and the lists of knowledgable specialists often do not agree precisely (e.g., compare the lists of boreal bird species of Johnson 1975, and Behle this symposium). I have followed Johnson's rather conservative designation of boreal bird species (for a list of these species and their distribution see Appendix 1). I have restricted my analysis to those species that he terms (again conservatively) "permanent resident Boreal species," be cause I wanted to include in my comparison with mammals only those species that maintain sedentary populations throughout the year. This eliminates from the analysis the large number of bird spe cies that breed on the montane islands but are likely to migrate or disperse long dis tances between successive breeding seasons. The definition of boreal mammal species in cludes those that inhabit juniper-pinyon woodland or habitats of higher elevation, but not the desert habitats of the Great Basin. I have excluded from the analysis large carnivores and ungulates because their dis tributions have been drastically altered by human activity and their original ranges and habitat requirements are poorly known. Also I have ignored bats, because their dis tributions are incompletely documented and they, like the migratory birds, probably are not permanent residents of the islands. The list of boreal mammal species (Appendix 2) is similar to that in Brown (1971), but it differs in some details because I have used slightly different criteria for designating bo real species and I have included a few more records of occurrence. The resulting lists of boreal bird and mammals contain species of generally similar body sizes and habitat re quirements, although there are approx imately 50 percent more mammal than bird species on both the large islands and the continents.

SPECIES—AREA RELATIONSHIPS

The number of species (S) inhabiting an island usually is positively correlated with insular area (A); this relationship takes the form $S = CA^z$, where the values of the constant (C) and slope (Z) depend on the characteristics of the specific taxon and group of islands under consideration (Mac-Arthur and Wilson 1967, Preston 1962). The slope of this relationship can indicate the relative importance of extinction and origi nation processes in determining the diver sity of insular biotas. (Barbour and Brown 1974, Brown 1971, MacArthur and Wilson 1967). Low slopes, $Z<0.20$, tend to charac terize samples of different areas within a continent, and the Z-value varies with envi ronmental heterogeneity (Harner and Har per, 1977). Islands usually have higher Z values; when the insular biota represents an approximate equilibrium between rates of colonization and extinction, Z-values tend to lie in the range 0.20-0.35. When there is no contemporary colonization to oppose extinc tion, islands tend to have even higher Z-values, often > 0.40. The reason for this pattern is straightforward. On continents small sample areas contain a significant pro portion of rare species. If these habitats were isolated and no immigration were per mitted, rare species would go extinct rapid ly on small islands and much more slowly on large ones, producing a much steeper species-area curve. Islands in equilibrium, where a significant rate of colonization op poses extinction, represent an intermediate

situation; species that go extinct on small islands tend to be replaced by colonists, but not at a sufficient rate to produce diversity comparable to that on continents. There can be exceptions to this pattern. For example, if only a small subsample of the continental biota is able to colonize a group of islands, the Z-value may be lower than expected because large islands will not acquire as many species as they can support (Barbour and Brown 1974).

This conceptual framework can be used to compare the species-area curves for the boreal birds and mammals. In my earlier analysis (Brown 1971), I argued that boreal mammals reached all of the islands during periods of climatic change in the late Pleistocene; since then there have been extinctions but no colonizations. This con-

clusion can be tested using a somewhat different data set for mammals and comparing the mammalian and avian distributions. If birds are better dispersers and are currently crossing the desert valleys to colonize the isolated peaks, then they should have a significantly lower Z-value than mammals. This is the case. The number of species of both birds and mammals is correlated significantly with area (Fig. 3, Tables 2 and 3). The Z-value for birds, 0.165, is even lower than that obtained for most insular biotas that are presumed to be in equilibrium and approximates values for continental samples. The Z-value for mammals, 0.326, is less than I obtained in my earlier analysis, $Z = 0.428$, and lies in the upper range of those observed for the biotas of true islands (MacArthur and Wilson 1967). Thus species-area
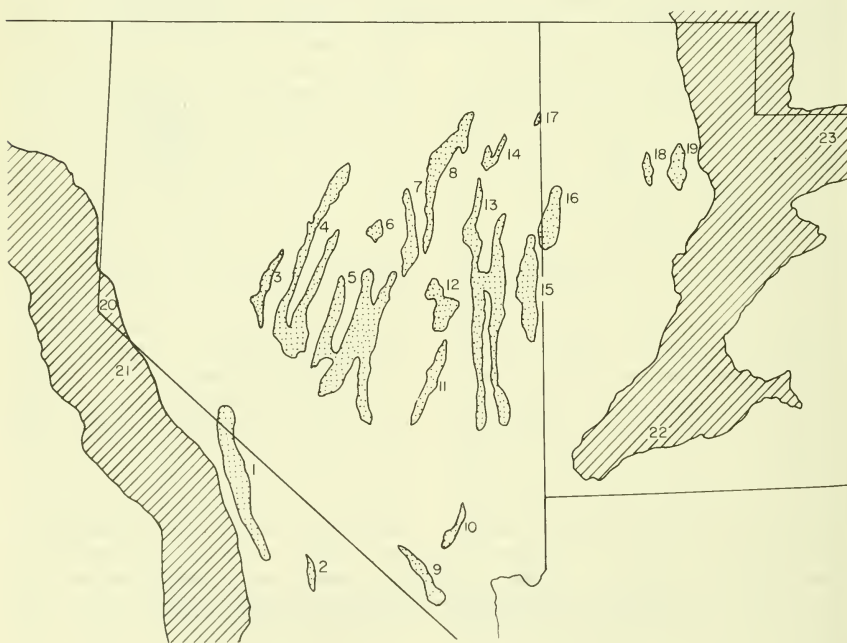

Fig. 3. The relationship of insular area to the number of permanent resident boreal bird species (above) and the number of small boreal mammal species (below). Note that the slope of the least squares regression line of the species-area curve for birds is much less steep than that for mammals. The equations for the fitted regressions and the correlation coefficients (r) are indicated.

curves for the boreal birds and mammals conform qualitatively to theoretical predictions, but they differ slightly from the quantitative Z-values that might be expected if the avian distribution represents an equilibrium between contemporary colonization and extinction, and the insular mammalian populations are Pleistocene relicts that do not disperse across the desert valleys.

These slight deviations from expected Z-values are not difficult to explain. The low Z-value for birds suggests that the isolation of the montane islands may not be a significant barrier to avian colonization. The facts that a) approximately 80 percent of the variation in insular bird species diversity can be accounted for by the combined effects of area and elevation (Table 2) or by habitat diversity (Table 3), and b) there appears to be no impoverishment of species numbers resulting from isolation by distance to the nearest continent (Table 2, and see next section) suggest that colonization rates are high and there is little if any effect of insular isolation. This is consistent with Johnson's (1975) conclusion that the diversity of boreal birds is attributable primarily to habitat; the impoverishment of the insular avifaunas is the result of reduced habitat diversity on the isolated peaks and not to any significant extent to low colonization rates. It should be noted that it is not necessary to infer from this that the desert valleys do not inhibit dispersal, only that colonization rates remain sufficiently high that boreal species which maintain breeding populations on the islands rarely go extinct and, if they do, they recolonize rapidly.

The fact that the Z-value for mammals also is slightly lower than predicted has a different explanation. As I shall show in the next section, the mammals that have colo-

TABLE 2. Stepwise multiple regression of the influence of three variables on the number of species of boreal birds and mammals inhabiting montane islands in the Great Basin.

	BIRDS			
Variable[1]	Order entered in equation	Contribution to R^2	F-value	Significance level
Area	1	0.4915	10.633	0.008
Highest peak	2	0.2836	12.607	0.005
Nearest continent	3	0.0051	0.201	0.658
	MAMMALS			
Variable[1]	Order entered in equation	Contribution to R^2	F-value	Significance level
Area	1	0.716	42.957	<0.001
Highest peak	2	0.005	0.271	0.610
Nearest continent	3	0.010	0.559	0.466

[1]Data are log-transformed data from Table 1.

TABLE 3. Correlation coefficients (r) between variables for the 13 montane islands for which all data are available. Upper right matrix is log-transformed data; lower left matrix is computed with untransformed data. Note that number of bird and mammal species are not closely correlated with the same variables.

	Area	Highest peak	Nearest continent	Habitat diversity	Bird species	Mammal species
Area	—	0.795	−0.079	0.623	0.701	0.891
Highest peak	0.778	—	−0.334	0.722	0.869	0.523
Nearest continent	−0.083	−0.224	—	−0.176	−0.367	−0.070
Habitat diversity	0.524	0.760	−0.102	—	0.851	0.539
Bird species	0.637	0.872	−0.310	0.898	—	0.611
Mammal species	0.876	0.817	0.090	0.542	0.592	—

nized the montane islands are those species of the continental fauna that occur at relatively low elevations within the boreal zone; species restricted to high elevations are absent from all of the isolated mountain ranges. The large islands, which also tend to have the highest peaks (Table 3), have extensive areas of mixed coniferous forest, wet meadow, and other high altitude habitats. Even with post-Pleistocene extinctions these mountains would be expected to support some of the mammal species characteristic of these habitats on the continental ranges. Thus, if the islands had an unbiased sample of the boreal mammal fauna, the larger islands should have more species than they do and the species-area curve would be steeper. In my 1971 paper, I reported a higher Z-value than obtained here. The reason is that I included in the present analysis some marginally boreal species (*Eutamias dorsalis, E. panamintinus,* and *Sylvilagus nuttalli*) that are characteristic of juniper-pinyon woodland and are present on most of the montane islands. This had the effect of adding an approximately constant number of species to the fauna of all islands, and thus lowering the slope of the exponential species-area relationship. This is the same effect that is produced by the disproportionate representation of low elevation species in the insular faunas relative to continental faunas because of differential colonization in the past.

Isolation and Paleoclimatic History

It is a common observation of insular biogeography that remote islands support fewer species than islands of comparable size and habitat diversity that are nearer to a continent (see MacArthur and Wilson 1967 and included references). This pattern is attributed to the limited ability of organisms to disperse so that the rate of immigration to an island declines with increasing isolation. In the present analysis, neither birds nor mammals demonstrate such a negative relationship between number of species and distance to the nearest continent (Tables 2 and 3). For mammals, this result is consistent with my 1971 analysis and conclusion that there is virtually no contemporary immigration to the isolated mountains because the desert valleys constitute almost absolute barriers to dispersal. The islands were colonized in the Pleistocene when periodic climate changes resulted in shifts in the altitudinal limits of the boreal vegetation. Data from plant macrofossils in woodrat middens suggest that, as recently as 8,000 to 12,000 years ago, periods of cooler, wetter climate enabled juniper-pinyon woodland to flourish at least 2,000 feet (600 m) below its present lower elevational limit (Wells and Berger 1967, Wells and Jorgensen 1964). This was sufficient to make juniper-pinyon and associated meadow and riparian habitats contiguous across virtually all of the Great Basin, and to enable the boreal mammals characteristic of these habitats to colonize all of the isolated mountain ranges. With the return of hotter, drier conditions, these "habitat bridges" connecting the islands to the continental ranges were eliminated and the insular mammalian faunas have been derived from the widespread Pleistocene fauna by independent extinctions on each island.

Several lines of evidence are consistent with this interpretation. 1) The relatively steep species-area curve (Fig. 3) suggests that extinction has played a major role in determining mammalian diversity. This is supported by the discovery of late Pleistocene fossils of at least one boreal species (*Marmota flaviventris*) from an island (Spring Range) where it no longer occurs (Wells and Jorgensen 1964). 2) The lack of any correlation between number of mammal species and distance to nearest mainland (Tables 2 and 3) or any other likely measure of insular isolation (Brown 1971) suggests that there is no contemporary immigration to the islands. 3) All of the species known from the islands are found in juniper-pinyon or other habitats of comparable elevation. It is possible to account

for the presence of the entire insular fauna in terms of colonization across habitat bridges that were known to have existed in the late Pleistocene. 4) All of the species of boreal mammals that are restricted to mixed coniferous forest or habitats of higher eleva tion on the continental ranges are absent from all of the montane islands, even though large areas of apparently suitable habitat are present on some of the larger is lands. These species include *Martes ameri cana, Aplodontia rufa, Eutamias alpinus, E. townsendi, E. speciosus, Tamiasciurus hud sonicus, T. douglasi, Glaucomys sabrinus, Phenacomys intermedius, Clethrionomys gapperi* and *Lepus americanus.* Paleobota nical evidence indicates that the habitats of these species were not connected across the Great Basin during the late Pleistocene. This is further evidence that small terrestri al mammals usually are unable to cross hab itat barriers only a few miles in extent and thus colonize isolated habitats only when bridges of appropriate habitat provide di rect access (Brown 1971, 1973).

The explanation for the lack of correla tion between number of species and dis tance to nearest continent in birds appears to be the opposite of that in mammals: birds are such good dispersers that they have colonized virtually all islands with suitable habitat regardless of their isolation. Both Johnson (1975) and Behle (this sym posium) report a negative relationship be tween their measure of insular isolation (cu mulative width of desert barriers) and number of permanent resident bird species, but both authors included continental sample areas in their analyses. The apparent effect of isolation in their analyses can be attributed largely to the fact that a signifi cantly greater number of species inhabit continental sites than occur on the islands; there is little or no effect of isolation by distance when only islands are considered (see Fig. 2 of Johnson 1975). This is con sistent with my own analysis of Johnson's and Behle's data. There is an insignificant negative correlation between number of

bird species and distance to nearest conti nent (Table 3), and the distance variable does not contribute significantly to account ing for number of bird species using mul tiple regression analysis (Table 2). It re mains to explain the difference in species diversity between the continents and islands. Some of those species present on the conti nents but absent from most of the islands may be limited in their distributions by their sedentary natures or their aversion to crossing inhospitable desert terrain. How ever, many of these species such as *Lagopus leucurus, Dryocopus pileatus,* and *Perisoreus canadensis,* have specialized habitat require ments and low population densities. Their habitats are totally lacking from many of the islands, and, even where they are pres ent, they often consist of small patches ob viously inadequate to support sustained populations. Two other sources of evidence suggest that rates of contemporary immigra tion by most boreal bird species are suffi ciently high to keep the habitats present on the islands filled with an appropriate com plement of species. First, such boreal bird species as *Picoides tridactylus* and *Cyano sitta stelleri,* which are restricted to high elevation, well-developed coniferous forests, are present on the islands. Since the habi tats of these species have not been con nected by bridges to the continental ranges during the Pleistocene, it must be inferred that at least these species are able to colo nize across significant barriers of unsuitable habitat. Second, vagrant individuals of some boreal species (e.g., *Cyanositta stelleri* and *Cinclus mexicanus*) infrequently are report ed significant distances from breeding popu lations (Johnson 1975, B. Bundick, pers comm.). This evidence indicates that even relatively sedentary permanent resident bo real birds are much more vagile than small boreal mammals.

DETERMINANTS OF SPECIES DIVERSITY AND COMPOSITION

Differences in dispersal account in large part for differences in the species-area rela

tionships between birds and mammals and in faunal composition between insular and continental mountain ranges (at least for mammals), but the considerable variation in species diversity among the insular bird and mammal faunas must be attributed primarily to ecological characteristics of the is lands. Although a common set of both bird and mammal species has had the opportunity to colonize virtually all islands, the iso lated mountain ranges support different numbers and kinds of species. Species diversity of both birds and mammals is closely correlated with insular area, but area is only a correlate of factors such as the quantity and diversity of habitat and food re sources that ultimately determine species diversity. Power (1972) and Johnson (1975) have shown for birds that someone familiar with a group of organisms can devise quantitative measures of habitat diversity that account for significantly more of the vari ance in insular species diversity than area. This approach has great utility for elucidating the environmental factors that influence the diversity and distribution of particular taxa, but it may not be useful for developing general biogeographic or ecological theory.

There are two arguments in favor of bas ing biogeographic theory on simple, stan dard parameters such as insular area. The first is practical. Parameters such as area, elevation (another correlate of habitat diversity), and distance to the nearest continent are easy to determine from maps. By obtaining these measurements and species lists from the literature, it is possible to describe clear patterns of plant and animal distribution without doing all the original fieldwork required to quantify accurately more direct environmental variables. Much of the recent synthetic work in insular biogeography has been done this way, and even those authors that have attempted to quantify variables such as habitat diversity often have used data available from the literature or topographic maps (e.g., Power 1972, Johnson 1975). The second argument is that area

may be the best parameter for constructing general theory that can be applied to di verse taxa and various kinds of islands. In the development of theory some sacrifice of precise explanation of specific cases usually must be made in order to obtain a desirable degree of generality. It is questionable whether it would be practical or profitable to base biogeographic theory on organism-specific parameters such as habitat diversity, food availability, or carrying capacity. Certainly at present we have no accepted, stan dardized techniques for measuring these variables in the field that are suitable for a variety of taxa and habitats.

Some test of the merit of this approach can be made by comparing the correlates of species diversity for boreal birds and mammals. Johnson (1975) developed a quantitative "habitat diversity score" that ac counted for most of the variability in the number of boreal bird species in his analysis. This appears to measure accurately the requirements of boreal birds in western North America, because Behle (this symposium) tested it and obtained gratifyingly similar results. Since boreal mammals utilize the same forest, meadow, and freshwater habitats as boreal birds, it would be encour aging if Johnson's habitat diversity score ac counted for similarly large proportions of the variability in insular species diversity for both taxa. Unfortunately this is not the case (Table 2). The number of boreal bird and mammal species inhabiting the same is lands are not very closely correlated ($r^2 \leq 0.37$); whereas 81 percent of the variability in bird species diversity can be attributed to habitat diversity score, the comparable fig ure for mammals is only 29 percent. Area is by far the best correlate of species diversity for both birds and mammals. When the ap propriate log-transformed data are used, area accounts for 49 and 79 percent of the variability in bird and mammal species numbers, respectively (Table 3). Inter estingly, elevation of highest peak (another correlate of habitat diversity readily obtain able from topographic maps) and area taken

together in multiple regression analysis (Table 2) account for almost as much variability in bird species diversity ($r^2 = 0.76$) as the habitat diversity score ($r^2 = 0.81$).

Two explanations can be offered for the lack of good correlation between Johnson's habitat diversity score and mammalian species diversity. First, the habitat diversity score is highly dependent on the species diversity of coniferous trees. Particular tree species and forest types probably are important to the boreal birds, but they are much less likely to influence the diversity of boreal mammals. As I have shown, boreal mammals that depend on the well-developed coniferous forests of high elevations have been unable to colonize any of the islands, and those mammals that have colonized, if they require conifers at all, are primarily species of the juniper-pinyon woodlands that are well developed on almost all of the islands. Second, Johnson's habitat diversity score is based primarily on the presence or absence of particular tree species or habitat types. This qualitative approach appears to work well for birds, because they have sufficiently high immigration rates to maintain populations on almost all islands where suitable habitats are present. In contrast, mammals, which have had to maintain insular populations for thousands of years in the absence of any significant immigration, may be much more dependent on the quantity of boreal habitats (particularly those characteristic of low elevations that were connected in the Pleistocene) which may be more closely correlated with insular area than with Johnson's more qualitative index. Whether one or both of these nonexclusive explanations turn out to be correct, it is clear that different factors determine the diversity of insular species of birds and mammals. These results suggest that parameters such as area, even though their effects are indirect and imprecise, may be the variables best suited for constructing and testing general biogeographic theory.

However, specific factors that influence the insular species diversity and composition of particular taxa can contribute to theory by providing information on the mechanisms and effects of the underlying processes of colonization and extinction. The great importance of habitat in determining insular bird species diversity, coupled with a low slope of the species-area curve and the lack of any significant effect of isolation by distance, suggests that boreal birds are able to disperse at a sufficient rate to maintain populations on most islands with suitable habitats. The distribution of boreal mammals presents a dramatic contrast. Mammal species are absent from many islands that have suitable habitats, either because they have never colonized or because they have gone extinct since the last episode of Pleistocene colonization. The interacting effects of habitat requirements and paleoclimatic changes in determining the set of species that colonized the islands already have been discussed. Of equal interest are the factors that have resulted in extinctions among the original colonists to produce the present insular faunas.

The mammalian faunas of the montane islands have been derived by extinction from a common set of 14 functional species that were widely distributed across the Great Basin during the late Pleistocene when their habitats were connected by bridges to the continental mountain ranges (Table 4). After the islands were isolated by the contraction of boreal habitats to approximately their present position, extinctions reduced the faunas of each island and thus played a major role in determining species composition. Five large islands have retained at least 10 of their original 14 species, but five small islands have lost all but 3 or 4 of the original set of species in the period of approximately 10,000 years that the boreal habitats have been isolated. The distribution of extinctions among species is highly nonrandom and appears to be related primarily to population size, as MacArthur and Wilson (1967) predicted. Herbivorous species of generalized habitat requirements and small to intermediate body size have persisted on

most of the islands (Table 4). In contrast, herbivores of large body size and/or specialized habitat requirements and carnivores have had higher extinction rates and persist on only a small proportion of the 19 islands. The frequency of occurrence of boreal species on the islands (Table 4) corresponds very closely to the relative abundance of these species where they occur together on large islands or continental mountain ranges (personal observations). The dependence of extinction on population size probably is even more precise than is apparent here, because population size is influenced by the presence of particular habitats and competing species which vary among islands. For example, one of the few mountain ranges where a juniper-pinyon chipmunk (*Eutamias dorsalis* or *E. panamintinus*) does not occur is the Ruby Mountains, where juniper-pinyon woodland is very poorly de-

veloped. Similarly, the chipmunk characteristic of higher elevations (*Eutamias umbrinus*) is absent from the Pilot Range, which has only small stands of mixed conifers on its single tall peak. On this mountain, in the absence of *E. umbrinus, E. dorsalis* has extended its altitudinal range upward into the mixed conifers on the peak.

CONCLUSIONS, PREDICTIONS, AND UNANSWERED QUESTIONS

The insular distributions of boreal birds and mammals in the Great Basin differ in ways that are consistent with both current biogeographic theory and independent evidence of ecological and historical factors that have affected colonization and extinction. All data seem consistent with the interpretation that insular bird populations represent an equilibrium between contem-

TABLE 4. Characteristics of the boreal mammal species that inhabit the montane islands of the Great Basin. Species are listed in decreasing order of frequency of occurrence.

Species	Body weight (grams)	Diet	Habitat	Number of islands inhabited
Eutamias umbrinus	60	mostly seeds	generalist: forests, wood-lands, talus	17
Neotoma cinerea	300	green vegetation	generalist: rock outcrops or talus in all habitats	17
Eutamias dorsalis, E. panamintinus	55	mostly seeds	generalist: primarily juniper-pinyon woodlands	16
Spermophilus lateralis	170	green vegetation seeds	generalist: open forest, meadow	14
Microtus longicaudus	45	green vegetation	generalist: meadow, open forest, streams	13
Sylvilagus nuttallii	800	green vegetation	generalist: all habitats except dense forest	12
Marmota flaviventris	3,000	green vegetation	generalist: open forest, meadow	10
Sorex vagrans, S. tenellus[1]	7	invertebrates	generalist: forest, meadow, streams	8
Sorex palustris	14	invertebrates	permanent streams	6
Ochotona princeps	120	green vegetation	talus adjacent to meadow	5
Zapus princeps	25	seeds, green vegetation	wet meadow, streams	4
Mustela erminea	50	small vertebrates	generalist: meadow, open forest	4
Spermophilus beldingi	300	green vegetation	wet meadows	3
Lepus townsendii	3,000	green vegetation	large open meadows	1

[1]Congeners listed on the same line are ecological and geographic replacements.

porary rates of colonization and extinction; immigration rates are sufficiently high that boreal bird populations inhabit almost all is lands where there are suitable habitats, re gardless of their isolation from continents. In contrast, the boreal mammal populations represent relicts of species that were wide spread in the Great Basin during the late Pleistocene when habitat bridges connected the islands and continents; the mammal faunas of the islands have been derived from a common set of Pleistocene colonists by subsequent extinctions in the absence of immigration.

Neither the avian nor the mammalian dis tributions fit the equilibrium model pro posed by MacArthur and Wilson (1967) to account for diversity on oceanic islands. The insular mammal faunas clearly are not in equilibrium; in the absence of immigra tion they are gradually relaxing toward an equilibrium of zero species at rates in versely related to island size. The distribu tion of birds does represent a sort of equi librium between contemporary colonization and extinction, but the immigration rates are so high that the islands are virtually sat urated with species for which the appropri ate habitats are present. The avifaunas of the islands differ from the MacArthur-Wil son model in that there is no significant ef fect of isolation by distance, species compo sition is quite precisely determined by habitat, and rates of faunal turnover prob ably are very low (see Brown and Kodric-Brown 1977).

The information available on the distribu tion of other vertebrates among insular hab itats suggests that the kinds of patterns de scribed here for birds and mammals may be widespread. Migratory birds, bats, and very large carnivorous and herbivorous mammals probably are at least as vagile as permanent resident boreal birds. They would be ex pected to colonize most suitable habitats and show little effect of insular extinction or isolation by distance. On the other hand, amphibians and reptiles probably have dis persal capacities similar to mammals. These

taxa are unlikely to cross habitat barriers of even modest extent, and it is well known that fishes can colonize new areas only when suitable habitat bridges are present (Barbour and Brown 1974, Hubbs and Mill er 1948, Hubbs et al. 1974, Smith, this sym posium). The distributions of these taxa should be extremely sensitive to paleocli matic and geological events; where insular habitats have been connected and reisolated they should show relictual distributions in which the identity of the colonists and the effects of subsequent extinctions produce patterns of diversity comparable to those of the small boreal mammals. It is interesting to speculate that the extremes of vagility which characterize most of the vertebrates and the extensive climatic and geological changes that have drastically changed the landscape of western North America within the last million years make it unlikely that land and fresh water vertebrates in this re gion will show the sort of equilibrium distri butions that have been demonstrated for the biotas of oceanic islands with a long history of isolation and relative environmental sta bility (see MacArthur and Wilson 1967, Simberloff 1974).

In insular biogeography many important questions remain to be answered, and much theoretical and empirical work is yet to be done before this promising and vigorous young science can afford to rest on its lau rels. The vertebrates that are distributed among the numerous isolated habitats in western North America continue to offer great potential as systems for testing theory and developing general concepts. For those organisms that appear to demonstrate equi librial distributions it is particularly impor tant to measure turnover rates accurately, and to incorporate the results into an ap propriate conceptual framework. For those organisms that exhibit relictual distributions it is important to elucidate patterns of colo nization and extinction and to relate those to theory. Three generations of icthyologists (Hubbs and Miller 1948, Hubbs et al. 1974, Smith, this symposium) have carefully dis-

sected historical changes in Great Basin drainages and have related them to the con temporary distribution of fishes. As yet there has been little attempt to relate these patterns to biogeographic theory, but the possibilities for doing so seem great and it is hoped it will be attempted soon. The distri butions of many organisms are patchy on scales smaller than the gross biogeographic one considered here. Smith (1974a, b) has obtained some encouraging results by using the theory of insular biogeography and the dynamics of opposing colonization and ex tinction rates to account for the distribution of a small boreal mammal (*Ochotona prin-ceps*) among the isolated patches of its spe cialized rockslide habitat in the Sierra Ne vada. It will be interesting to see to what extent this approach continues to prove use ful for understanding insular distributions on various scales.

Acknowledgments

APPENDIX 1. Records of occurrence of permanent resident boreal bird species.[1]

Species	Sample Area																
	1	2	3	4	8	9	10	11	14	15	16	18	19	20	21	22	23
Dendragapus obscurus	x			x	x			x	x	x	x	x	x	x	x	x	x
Bonasa umbellus																x	x
Lagopus leucurus																	x
Oreortyz picta	x	x		x										x	x		
Glaucidium gnoma		x				x								x	x	x	x
Strix occidentalis														x	x	x	x
S. nebulosa															x		
Dryocopus pileatus															x	x	x
Dendrocopus villosus	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
D. pubescens					x					x	x	x	x			x	x
D. albolaruatus														x	x		
Picoides arcticus														x	x		
P. tridactylus										x						x	x
Perisoreus canadensis																x	x
Cyanositta stelleri	x		x			x		x		x	x	x	x	x	x	x	x
Parus gambeli	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Sitta carolinensis	x	x	x	x	x	x	x	x	x	x	x			x	x	x	x
S. pygmaea	x					x	x			x				x	x	x	x
Cinclus mexicanus	x			x	x	x				x	x	x	x	x	x	x	x
Pinicola enucleator														x	x	x	x
Total	8	5	4	6	6	6	5	5	4	9	7	6	6	13	15	15	16

[1]Data from Johnson (1975) and Behle (this symposium).

APPENDIX 2. Records of occurrence of small boreal mammal species.[1]

Species	Sample Area 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Sorex lyelli																					x		
S. trowbridgei																				x	x		x
S. vagrans[2]	x			x				x	x				x		x	x				x	x	x	x
S. tenellus	x				x				x						x					x	x	x	x
S. palustris	x			x	x	x		x				x			x			x		x	x	x	x
Martes americana	x			x																x	x	x	x
Mustela erminea	x		x	x											x					x	x	x	x
Aplodontia rufa																				x	x	x	x
Marmota flaviventris	x		x	x	x			x				x	x	x	x	x		x		x	x	x	x
Spermophilus armatus																					x		x
S. beldingi				x	x		x	x									x			x	x		x
S. lateralis	x		x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x
Eutamias alpinus																					x		
E. townsendii																				x	x		
E. dorsalis	x			x	x		x			x	x	x	x	x	x	x	x	x	x	x	x	x	x
E. amoenus																				x	x		
E. quadrimaculatus																				x	x	x	
E. quadrivittatus																						x	
E. umbrinus[2]	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x			x	x
E. panamintinus																					x		
E. speciosus																				x	x	x	x
Tamiasciurus hudsonicus																							x
T. douglasii																				x	x	x	x
Glaucomys sabrinus																				x	x	x	x
Neotoma cinerea	x		x	x	x		x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x
Phenacomys intermedius																							x
Clethrionomys gapperi																				x			x
Microtus longicaudus	x		x	x	x	x		x			x	x	x		x	x		x		x	x	x	x
M. richardsoni																			x				x
Zapus princeps				x		x		x												x	x		x
Ochotona princeps	x		x	x	x			x												x	x	x	x
Lepus townsendii								x												x	x	x	x
L. americanus																				x		x	x
Sylvilagus nuttallii	x	x	x	x	x			x	x	x	x	x	x		x	x				x	x	x	x
Total	11	3	7	13	10	4	4	12	6	3	5	7	8	4	10	8	3	6	6	22	23	16	21

[1]Data from Durant (1952), Durant et al. (1955), Grinnell (1933), Grinnell and Storer (1924), Hall (1946), Museum of Zoology at the University of Utah, and my own field work.
[2]Includes Sorex obscurus.
Includes Eutamias palmeri.

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